

## Morphometric variation of the common shrew *Sorex araneus* in Ukraine, in relation to geoclimatic factors and karyotype

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**ABSTRACT.** Comparisons were made of chromosomal and macro-morphological variation in two wide-spread chromosome races of the common shrew *Sorex araneus* Linnaeus, 1758 in the Ukraine using multivariate statistics. Representatives of the Kiev and Neroosa races cannot reliably be identified from craniometric characteristics. Within the two chromosome races, however, we observed a relationship between morphology and geography. About 60% of morphological variance could be explained by the influence of geoclimatic factors. It was confirmed that ecogeography is more important than karyotype as a morphological determinant in the common shrew. Highly differentiated southern Ukrainian forms of *S. araneus* may be regarded as ecotypes.

**KEY WORDS:** *Sorex araneus*, morphometrics, geoclimatic factors, chromosome races.

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## Морфометрическая изменчивость обыкновенной бурозубки *Sorex araneus* на территории Украины в связи с геоклиматическими факторами и кариотипом

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**РЕЗЮМЕ.** С помощью методов многомерной статистики выполнено сопоставление хромосомного и макро-морфологического уровней изменчивости у двух широко распространенных хромосомных рас обыкновенной бурозубки *Sorex araneus* Linnaeus, 1758. Оказалось, что представители хромосомных рас Киев и Нерусса почти неразличимы морфологически по комплексу краниометрических характеристик. В то же время, в пределах обеих хромосомных рас были отмечены общие тенденции географической изменчивости комплекса краниометрических признаков. Около 60% морфологической изменчивости может быть объяснено влиянием геоклиматических факторов. Подтверждено, что эко-географическая принадлежность является более значимым морфологическим детерминантом у обыкновенной бурозубки, нежели различия кариотипа. Высоко дифференцированные южные формы *S. araneus* рассматриваются как экотипы.

**КЛЮЧЕВЫЕ СЛОВА:** *Sorex araneus*, морфометрия, геоклиматические факторы, хромосомные расы.

### Introduction

The common shrew *Sorex araneus* Linnaeus, 1758 is known as one of the most variable species of the genus *Sorex* with respect to morphology and karyology.

Intensive investigation of *S. araneus* karyology has revealed about 70 chromosome races in Europe and Siberia (Wójcik *et al.*, 2002). The extent to which karyological and morphological differentiation coincide has been studied in different regions over the vast species range (Hausser, 1984; Zima & Král, 1985; Searle & Thorpe, 1987; Hausser *et al.*, 1991; Meyer & Searle, 1994; Chętnicki *et al.*, 1996; Wójcik *et al.*, 2000; Banaszek *et al.*, 2002; Polyakov *et al.*, 2002; Okulova *et al.*, 2004). It has been demonstrated that differences in morphology do not conform to the geographical distribution of chromosome races of *S. araneus* (Zima & Král, 1985), and could be explained

rather by differences in environmental conditions (Sulka-va *et al.*, 1985; Wójcik *et al.*, 2000). In some cases however, significant morphological differences have been detected between neighbouring chromosome races (Chętnicki *et al.*, 1996; Polyakov *et al.*, 2002). In Siberia, chromosome differentiation of the common shrew has been found to coincide with subspecies division (Polyakov *et al.*, 2002; Okulova *et al.*, 2004).

In Ukraine, three chromosome races of *S. araneus* have been identified (Mishta *et al.*, 2000). Two of them, the Kiev (XX/XY<sub>1</sub>Y<sub>2</sub>, af, bc, hi, g/m, k/o, n, p, q, r) and the Neroosa (XX/XY<sub>1</sub>Y<sub>2</sub>, af, bc, hi, g/o, k/r, m/n, p/q), occur respectively on the right and left banks of the Dnieper River.

In 1913 Thomas described a subspecies of the common shrew from the Danube delta: *S. araneus peucinius* Thomas. This form was distinguished from other *S. araneus* subspecies in its extremely large hind leg,

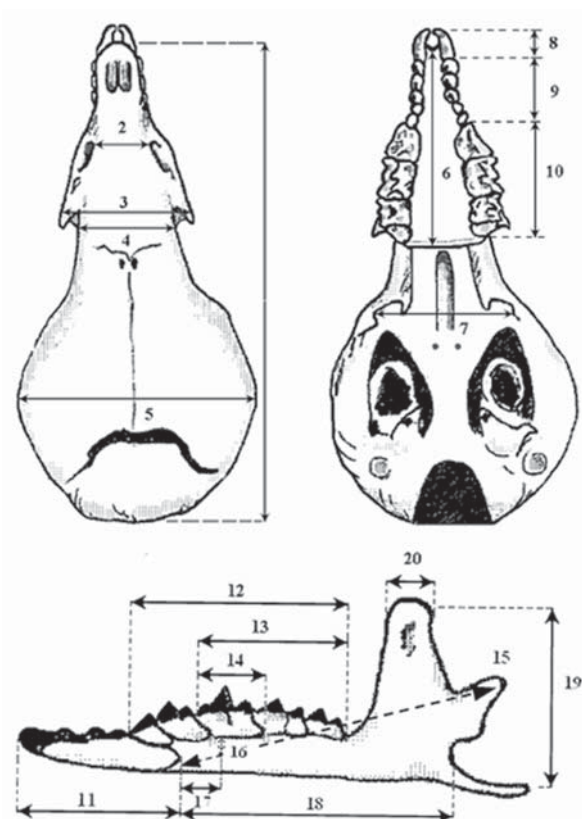


Figure 1. Measurements performed on skull and mandible. 1 — condylobasal length; 2 — breadth between lacrimal foramina; 3 — maxillary breadth; 4 — interorbital breadth; 5 — cranial breadth; 6 — palatal length; 7 — postglenoid width; 8 — length of the upper incisor; 9 — length of the upper antemolars; 10 — length of the upper molariform teeth; 11 — length of the lower incisor; 12 — length of the mandibular toothrow (except incisor); 13 — length of m1–m3; 14 — length of m1; 15 — length of the mandible (to the end of mandibular condyle); 16 — distance from m1 to mental foramen; 17 — distance from i1 to mental foramen; 18 — length of the horizontal branch of the mandible; 19 — height of the mandible; 20 — breadth of the coronoid process.

peculiarities of its dentition and its monochromatic winter fur colour (Thomas, 1913, cited in Ognev, 1928). Later, another southern subspecies of *S. araneus* was described from the Dnieper delta — *S. araneus averini* (Zubko, 1936, cited in Abelentsev *et al.*, 1956). However, since then it has been regarded as pointless to try to classify shrews from the lower reaches of the Dnieper River into subspecies until proper taxonomic studies are conducted, given that all of the animals are generally the same size as *S. a. peucinius* (Migulin, 1938; Abelentsev *et al.*, 1956). Thus, investigators have not reached a consensus about the variability and differentiation of *S. araneus* over the territory of the European part of the Former Soviet Union, and the Ukraine in particular. Some authors (Ognev, 1928; Migulin, 1938; Abelentsev *et al.*, 1956; Mezherin *et al.*, 1984) accept the existence of different subspecies in Ukraine, others (Gureev, 1957; Dolgov, 1985) do not attach importance to any differences observed, regarding variability in *S. araneus* as continuous.

To examine morphological differentiation in the common shrew over the southern part of Eastern Europe, I investigated a complex of craniometric features using multivariate statistics and placed the results in the context of geography and karyotype.

## Material and methods

A set of 20 measurements of immature common shrews were taken on the right side of the skull (Fig. 1). In total 223 skulls from different localities in Ukraine, Moldova, Belarus and Romania were analysed (Tab. 1, Fig. 2). Measurements were made using a micrometer eyepiece scale (0.01 mm) on a binocular microscope.

**Statistical treatment.** For the analysis of mandible measurements, I used univariate and multivariate statistics.

The influence of external factors on morphological variability (geographic origin, affiliation to the chromosome race — if known — and sex) was determined with univariate ANOVA. All external factors were considered as fixed.

To account for correlated characters, trends of variation and differentiation in *S. araneus* were explored using principal component analysis (PCA). Eigenvectors and eigenvalues were calculated on the basis of the variance-covariance matrix.

In order to test whether the intraspecific variance was distributed randomly for all the principal components obtained, the part of this variance accounted for



Figure 2. Geographical origin of the material (localities numbered as in Tab. 1). Kiev chromosome race — black circles; Neroosa chromosome race — white circles; uncertain race affiliation — grey circles.

Table 1. Geographical origin and other details of samples (samples listed from north to south).

No.	Sample name	Geographical origin	<i>N</i>	Race	Collection
1	Belarus	Belarus: Gomel Province, Abakumy vic., Loev	10	–	DEB
2	Chernyiv	Ukraine: Chernyiv Province, Kozeletsk District	14	–	KSU
3	Volyn	Ukraine: Volyn' Province, Shatsk vic.	4	–	KSU
4	Sumy	Ukraine: Sumy Province, Yampil District, Lebedyn District	9	NE	KSU
5	Zhytomir	Ukraine: Zhytomir Province	11	KI	NHM
6	Kiev	Ukraine: Kyiv vic., Teremky	20	KI	DEB, KSU
7	Kaniv	Ukraine: Cherkassy Province, Kaniv State Reserve	20	–	MSU, DEB
8	Kharkiv	Ukraine: Kharkiv Province, Zmijiv vic.	9	NE	MSU
9	Khmelnitsky	Ukraine: Khmelnytsky Province, Volochynsky District	5	KI	NHM
10	Kirovograd	Ukraine: Kirovograd Province, Znamensky District	4	–	NHM
11	Lugansk	Ukraine: Lugan'sk Province, Kremenets District	20	NE	KSU
12	Karpaty	Ukraine: Transcarpathians, Rakhiv District, Petros Mt.; Tiachevsky District; Ivano-Frankivsk Province, Nadvorna District	20	KI	DEB, USU, KSU
13	Donetsk	Ukraine: Donets'k Province, Atamans'ka Village	4	NE	MSU
14	Moldova	Moldova: Kagul vic., Manta Lake	20	KI	CM
15	Kherson	Ukraine: Kherson Province, Gola Prystan' District, Ivano-Rybalche	12	NE	KSU, MSU
16	Golaya Pristan'	Ukraine: Kherson Province, Gola Prystan' District, Velykyi Potiomkinsky Island	22	NE	KSU
17	Odessa	Ukraine: Odessa Province, Vilkovo vic., islands of Kilijskaya delta	25	KI	CF
18	Romania	Romania: Danube delta	20	–	CF

Race: NE — Neroosa; KI — Kiev

DEB — collection of the Department of Ecology and Biogeography of Schmalhausen Institute of Zoology NAScU;

KSU — Zoological Museum of Kiev State University;

MSU — Zoological Museum of Moscow State University;

USU — Zoological Museum of Uzhgorod State University;

MNH — National Museum of Natural History of Ukrainian Academy of Sciences Ukraine;

CM — private collection of Mikhailenko A.G.;

CF — private collection of Fedorchenko A.A.

by each component was compared to a broken stick distribution using the Kolmogorov-Smirnov goodness of fit test. This theoretical distribution specifies the distribution of a finite quantity partitioned at random (see Hausser, 1984).

To test whether adaptations to local environmental conditions play an important role in morphological differentiation, a multiple regression analysis of each morphological variable against nine geoclimatic variables was carried out. Residuals obtained were also analysed using principal component (PCA) and discriminant function (DFA) analyses.

Interdependence between geoclimatic factors and individual morphological characters was studied using multiple regression analysis. The geoclimatic factors used in the study are presented in Tab. 2. Climatic data from the weather stations nearest each sample point were taken from the Geographical Encyclopaedia of Ukraine (1989, 1990, 1993).

The interdependence of two multivariate data arrays of craniometric and geoclimatic variables was determined by use of canonical correlation analysis.

Statistical analysis was performed using the Statistica 6.0 package (StatSoft Inc., 1984-2001, USA).

Chromosome races:

1. Kiev race ( $XX/XY_1Y_2$ , *af, bc, hi, g/m, k/o, n, p, q, r*)

Table 2. Geoclimatic factors used in the study.

Characteristic	Abbreviation
Latitude	LAT
Longitude	LONG
Altitude	ALT
Average temperature of January	TEMP_J
Average temperature of June	TEMP_I
Average annual range of temperatures	TEMP_D
Average annual number of days with temperature exceed 10°C	W_DAYS
Average snow depth	SNOW
Average annual precipitation	RAIN

2. Neroosa race (XX/XY<sub>1</sub>Y<sub>2</sub>, *af, bc, hi, g/o, k/r, m/n, p/q*)

The details of racial distribution and chromosome polymorphism in the study area have been described elsewhere (Mishta *et al.*, 2000). The approximate geographic distribution of the two races in the region studied is shown in Fig. 2. Samples used to analyse the relationships between karyotypic and macro-morphological differentiation are presented in Tab. 1. I analysed material from localities where karyotyping took place or from localities situated in core of the known race distribution. Material of uncertain racial affiliation was excluded from the analysis.

For convenience of analysis, all populations were conditionally separated into “northern” and “southern” subgroups. Populations of Moldova, Odessa, Romania, Golaya Pristan’ and Kherson were classed into a “southern” subgroup and the remaining populations were considered “northern”.

Populations were also simplistically divided into “western” and “eastern” subgroups, which approximates with the chromosome races. In the “western” subgroup representatives of the Kiev race (Zhytomir, Kiev, Khmelnytsky, Moldova, Odessa) as well as populations of uncertain racial affiliation (Kirovograd, Kaniv, Romania) are included. The “eastern” subgroup includes representatives of the Neroosa race (Sumy, Kharkiv, Lugansk, Kherson, Golaya Pristan’) and also the Belarus and Chernigiv populations of uncertain racial affiliation.

## Results and discussion

Mean values and standard deviations of 20 craniometric variables of *S. araneus* are presented in Appendix 1. Univariate ANOVA of all craniometric characters did not reveal differences in mandible size between males and females, except for interorbital breadth ( $p < 0.05$ ). At the same time it was demonstrated that differentiation of populations in the set of characters studied was best associated with geographical origin (for 19 craniometric characters out of 20:  $p < 0.001$ ; except for the distance between il and the mental foramen).

**Trends in craniometric variation in the common shrew.** To study more precisely the geographic differentiation of *S. araneus* populations, comparative analysis of shrews from different regions of Ukraine and neighbouring territories was carried out using principal components analysis. We analysed six principal components (PCs), which altogether describe 77.19% of variance in the dataset. The positive end of each PC has shrews with the largest skulls, and the negative values are associated with the smallest skulls. Component loadings for craniometric characters of *S. araneus* are presented in Appendix 2.

The PC1 explains 51.54% of total variance. The most important characters for separating *S. araneus* populations on this component are condylobasal length, length of the mandible to the end of mandibular condyle, length of the horizontal branch of the mandible, palatal

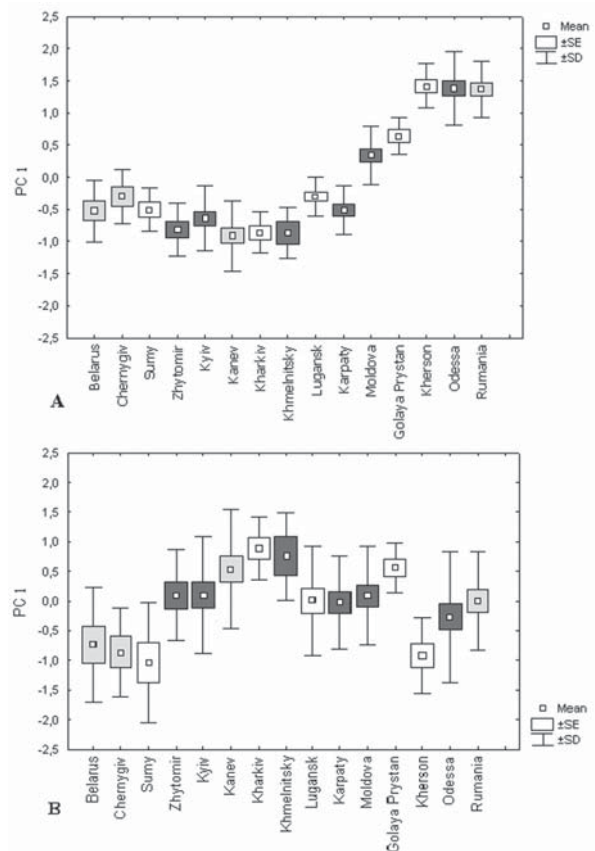


Figure 3. Geographical variation of normalized values of principal components: original morphological variables (A); their residuals after removing the effect of nine geoclimatic variables (B). Samples are ranked from left to right according to their geographical location from north to south and marked with colour according to their racial affiliation (see Fig. 2). Kiev chromosome race — black; Neroosa chromosome race — white; uncertain race affiliation — grey.

length, length of the upper molariform teeth, length of the mandibular tooththrow (except incisor), length of m1-m3 and height of the mandible. Maxillary and cranial breadth and the length of m1 contribute a smaller loading.

PC1 had a positive loading on all characters, which means that positive component values correspond to larger variable values and that PC1 is essentially a “size” component. Fig. 3A shows mean PC1 scores for samples ordered from left to right according to their geographic location from north to south. One can see that within the “northern” subgroup of populations (Belarus-Lugansk), the difference between mean values of the component is not significant. Populations from islands in the Danube delta (Romania, Odessa) and the Dnieper delta (Kherson) are substantially differentiated from populations of “northern” Ukraine. The Moldova population and the “continental” population of the Kherson region (Golaya Pristan’) have an intermediate position. Thus, the magnitude of the craniometric charac-



ters of *S. araneus* (determined by PC1) increases in a southerly direction. In addition to this, differentiation between neighbouring populations is more noticeable in the south.

It is evident that populations of *S. araneus* are to a great extent differentiated by PC1, which represents general proportions of the skull. In both the Neroosa (Sumy, Kharkiv, Lugansk, Golaya Pristan', Kherson) and Kiev (Zhytomir, Kiev, Khmelnytsky, Karpaty, Moldova, Odessa) chromosome races there are parallel trends of geographical variation (Fig. 3A).

PC2 explains 6.94% of the total variance. The largest contributions to the second component are made by the length of the upper incisor, the distance from i1 to the mental foramen and the length of the lower incisor. Thus, this component reflects the relative length of incisors against the distance from i1 to the mental foramen. The mean values do not vary systematically by geographical location. Mean values of this PC demonstrate large differences among shrews from western Ukraine: Khmelnytsky-Karpaty. Shrews from the Karpaty population are characterized by relatively long incisors and a very small distance from i1 to the mental foramen and shrews from Khmelnytsky show the reverse.

PC3 explains 5.54% of the total variance. The largest contribution to the third component is made by the distance from i1 to the mental foramen, the breadth between the lacrimal foramina and the interorbital breadth. On this component, populations from "eastern" Ukraine are slightly differentiated from populations of "western" Ukraine. The mean values of this component also suggest a slight differentiation of the Moldova population within the "western" group.

PC4 explains 4.94% of the total variance. The largest contributions in the values of the fourth component are made by the distance from m1 to the mental foramen and the breadth of the coronoid process. In this case there is also a slight differentiation between representatives of "western" and "eastern" Ukraine. The mean values of this PC suggest a slight differentiation of the Kherson population within the "eastern" group.

PC5 explains 4.48% of the total amount of morphological variance. The mean values do not vary systematically by geographical location. The largest contribution in the values of this component is made by the length of the upper incisor.

PC6 accounts for only 3.76% of the variation. There was a substantial loading on the postglenoid width. The mean values of this component suggest a separation of the Khmelnytsky population.

To consider again the best example of geographic variation in PC scores, the increasing scores from north to south in PC1 (Fig. 3A) suggest that the main cause of morphological differentiation in the Ukraine is adaptation to the local environment. To test this hypothesis, a multiple regression analysis of each morphological variable against the nine above mentioned geoclimatic characteristics was performed to obtain residual morphological variables uncorrelated with these geoclimatic

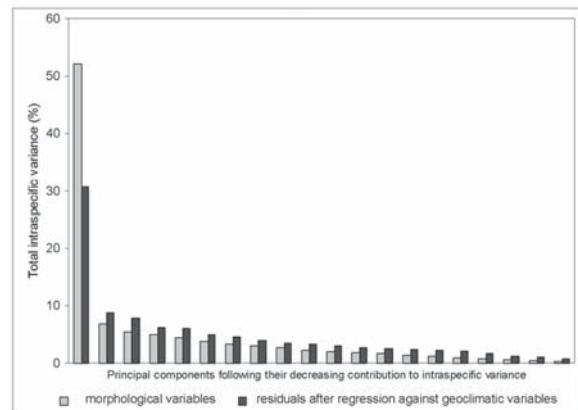


Figure 4. Distribution of the intraspecific variance of the principal components computed on the original morphological characters and their residuals after removing the effect of nine geoclimatic variables. Principal components are ranked following their decreasing contribution to intraspecific variance.

characteristics. In Fig. 4 the partitioning of the total intraspecific variance among the untransformed principal components is compared with their residuals after removing the effect of the nine geoclimatic factors. A Kolmogorov-Smirnov test indicates that the first of these two distributions shows departure from normality ( $p < 0.01$ ), while the second one does not differ significantly from expectation ( $p < 0.1$ ). Furthermore, the residuals no longer show the same geographical pattern as the untransformed principal component scores (Fig. 3B).

So, the general geographic trend of the complex of correlated craniometric characters within Ukrainian common shrews has been revealed. Overall, with some exceptions, these characters show a latitudinal gradient.

**Contributions of geoclimatic characteristics in differentiation of the common shrew.** Geographic variation in the complex of craniometric variables studied was greater in southern regions of Ukraine, where environmental pressure is greatest (Geographical Encyclopaedia of Ukraine, 1989, 1990, 1993).

The morphological clines, which are expected from the gradual geoclimatic clines throughout the studied area, are best displayed by means of a canonical correlation analysis. Correlations between the 20 macromorphological variables and 9 geoclimatic characteristics were obtained. The relationships between the canonical functions of the craniometric and the geoclimatic variables are presented in Tab. 3 and the loadings for these functions are presented in Appendix 3.

The part of the total morphological variance explained by the geoclimatic function is 71.4%. As shown in Tab. 3, the canonical correlation coefficients between the first, second, third and fourth pairs of canonical functions are highly significant. This implies that at least 60.9% of variance of the complex of craniometric

Table 3. Relationships between the canonical functions of craniometric and geoclimatic variates.

Pair of Canonical functions	Eigenvalue	Canonical correlation				Variance explained (%)	
		R	$\chi^2$	df	<i>p</i>	MORPH	GEOCL
1	0.774	0.879	715.92	180	<0.0001	48.26	50.86
2	0.425	0.651	407.89	152	<0.0001	4.10	7.69
3	0.352	0.593	293.41	126	<0.0001	3.87	13.08
4	0.296	0.544	203.57	102	<0.0001	2.57	3.00
5	0.224	0.473	130.80	80	<0.001	2.08	11.02

variables is highly correlated with geoclimatic variation.

The first morphological variate accounted for 48.26% of the total morphological variance, 50.86% of which can be attributed to the geoclimatic variables. The remaining four functions explained only a lower percentage of the morphological variability (Tab. 3).

The contributions of different geoclimatic variables (Appendix 3b) demonstrate that the average annual range of temperatures has the greatest influence on the craniometric complex factor MORPH1 (Tab. 3). Those most related to the temperature factor variables are condylobasal length, maxillary breadth, palatal length and overall length of mandible (Appendix 3a).

The canonical variate analysis revealed that canonical functions of morphological and geoclimatic variates correlate significantly and obvious clinal variation of the complex of craniometric characteristics exists.

The combination of larger dimensions of craniometric features towards the south together with separation of *S. araneus* populations in the south suggests that adaptation to local environmental conditions could explain macro-morphological differentiation in *S. araneus*.

To verify this hypothesis, I carried out a multiple regression analysis of the set of variables (20 craniometric and 9 geoclimatic characteristics taken together). Affiliation to the "southern" or "northern" subgroup was used as the dependent variable. Separation into "southern" and "northern" subgroups is significantly associated with the whole complex of geoclimatic factors (for all characteristics excluding altitude  $p < 0.0001$ ) (Tab. 4). Among the craniometric characteristics included in the model we can see influences from postglenoid breadth (#7,  $p < 0.001$ ), condylobasal length (#1,  $p < 0.05$ ), maxillary breadth (#3,  $p < 0.05$ ), palatal length (#6,  $p < 0.05$ ), length of the mandibular toothrow (#12,  $p < 0.05$ ), distance from m1 to mental foramen (#16,  $p < 0.05$ ) and breadth of the coronoid process (#20,  $p < 0.05$ ).

**Macro-morphological differences between shrews of different chromosome races.** The relationships between chromosome races of the common shrew in Europe as a whole and in Eastern Europe in particular is a subject of wide speculation (Searle, 1984; Wójcik, 1993; Searle & Wójcik, 1998; Orlov *et al.*, 2004). No doubt, as our knowledge of the diversity of chromosome races increases, it will be necessary to

revise previous phylogenetic schemes. The chromosome races under study likely represent different subgroups within the previously described West European Karyotypic Group (WEKG); the Neroosa race can be placed in a new group, which would be closely united with chromosome races from East Europe. The relationships between chromosome races of the common shrew in the region studied and in adjacent territories will be the subject of a later publication (work in progress).

Univariate ANOVA showed that six characters out of 20 differ significantly between chromosome races:

Table 4. Craniometric and geoclimatic characteristics which determine division to southern and northern subgroups in the common shrew ( $R = 0.98$ ,  $R^2 = 0.97$ ,  $p < 0.0001$ ).

Variable	B	$t_{201}$	<i>p</i>
Intercept	-1.340	-4.340	<0.0001
TEMP_D	-0.298	-11.657	<0.0001
12	0.159	2.107	<0.05
W_DAYS	-0.008	-12.838	<0.0001
1	0.048	2.310	<0.05
7	0.090	3.205	<0.001
TEMP_J	0.499	15.096	<0.0001
TEMP_I	0.378	15.421	<0.0001
RAIN	0.001	5.259	<0.0001
LONG	0.020	4.459	<0.0001
3	-0.141	-3.514	<0.0001
16	0.186	2.258	<0.05
20	0.138	1.931	0.054
SNOW	-0.006	-4.222	<0.0001
6	-0.093	-3.038	<0.05
ALT	0.047	2.122	<0.05
8	0.094	1.243	0.215
19	0.061	1.391	0.165
13	0.126	1.515	0.131
18	0.085	1.889	0.060
11	0.064	1.461	0.145
15	-0.046	-1.103	0.271

Table 5. Classification results of the discriminant analysis of the 20 morphological variables and the residuals remaining after regression of the morphological variables by the geoclimatic factors.

Actual race	Predicted race membership (% and number)					
	Morphological variables			Residuals		
	%	Kiev	Neroosa	%	Kiev	Neroosa
Kiev (n=101)	92.079	93	8	91.089	92	9
Neroosa (n=45)	76.363	13	42	40.000	33	22
Total	86.542	106	50	73.077	125	31

length of m1 ( $p<0.001$ ), length of m1–m3 ( $p<0.01$ ), distance from m1 to mental foramen ( $p<0.01$ ), interorbital breadth ( $p<0.01$ ), maxillary breadth ( $p<0.05$ ) and length of the upper antemolars ( $p<0.05$ ). Only one of these characteristics – distance from m1 to mental foramen – does not have a longitudinal geographic trend, so it could truly reflect genetic differences between the races.

At the level of chromosome differentiation here (at least three chromosome rearrangements), morphological differences between representatives of two chromosome races of *S. araneus* were found to be insignificant. Only one measurement could be linked to genetic differentiation; the rest are associated with geographical variation and have a high correlation with geoclimatic factors.

This statement is confirmed by discriminant function analyses of 20 morphological variables and their residuals after regression by geoclimatic ones. In the first case analysis led to the correct classification in approximately 87% of cases (Tab. 5). Specimens of the Kiev race were correctly classified in 92% of cases, and those from the Neroosa race in 76% of cases. The discriminant function explained 4.43% of the total morphological variance between the two studied chromosome races of shrews. The value of  $\chi^2$  test obtained by transformation of Wilk's lambda was statistically significant ( $\chi^2=148.53$ ,  $p<0.0001$ ). Standardized coefficients of the discriminant function for morphological variables were established. Variables such as maxillary breadth, interorbital breadth, length of the upper incisor, length of the upper antemolars, length of m1–m3, length of m1, distance from m1 to mental foramen, length of the horizontal branch of mandible and breadth of the coronoid process had important contributions for the discriminant function. Thus, it can be suggested that these variables account for most differences in mandible morphology between the two chromosome races. At the same time, the discriminant function analysis of residuals enables us to obtain a clear classification of individuals according their racial affiliation:  $\chi^2=21.63$ ,  $p=0.36$  (Tab. 5). In this case, only 73% of individuals were assigned to their actual chromosome races correctly.

So, our results do not show clear relations between morphometric variation and racial affiliation in Ukrainian *S. araneus*. Differences observed in this study may represent variation among western and eastern groups of populations rather than between representatives of different chromosome races.

Numerous previous investigations have demonstrated that the differentiation of karyotypes between populations from different geographical localities does not correlate with phenotypic variation (Zima & Král, 1985; Searle & Thorpe, 1987; Meyer & Searle, 1994; Wójcik *et al.*, 2000). Even shrews from the Scottish island of Islay, which could be distinguished by nonmetrical (karyological and genetic) techniques, could not be separated from other British *S. araneus* by metric features (Meyer & Searle, 1994).

Our results confirm the statement of Wójcik *et al.* (2000) that karyotypic divergence does not play an important role in differentiating skull morphology among chromosome races of *S. araneus* of a given region, and that geography is more important than karyotype as a morphological determinant.

However, it has also been demonstrated (Chętnicki *et al.*, 1996; Polyakov *et al.*, 2002; Okulova *et al.*, 2004) that when the level of karyotype differentiation is higher, morphological differences between chromosome races of *S. araneus* become more visible.

**Southern populations of the common shrew and possible causes of their macro-morphological distinctiveness.** In the last century, numerous subspecies of *S. araneus* have been distinguished in Europe, which Zalesky (1948) divided into two main groups: “*araneus*” in the north and “*tetragonurus*” in the south. The basis of this division was a difference in general body size and peculiarities of fur coloration. The distribution range of the southern forms roughly coincides with the area occupied by vineyards. Notwithstanding the fact that several of populations included in the “*tetragonurus*” group are now recognized as different species (*S. coronatus*, *S. antinorii*, *S. granarius*, *S. arunchi* and *S. samniticus*), the basic idea of the division of *S. araneus* into these two groups remains subject to scrutiny.

According to Niethammer & Krapp (1990) the description of numerous subspecies within the “*tetragonurus*” group and in marginal regions of the global distribution of the “*araneus*” group could be explained both by altered ecological conditions and above all by isolation in mountain regions. It is worth noting that only one northern European subspecies has been described: *S. araneus bergensis* Miller from Norway, which was isolated during the last glaciation.

Dehnel (1950) considered the central and north-European populations of *S. araneus* to be genetically connected to forms that persisted in the glacial periods near ice-sheet borders. Common shrews from southern Europe lost contact with the northern group probably in the last glacial period, owing to the zone of dry and cold steppe stretching across Europe from East to West and reaching almost to the Pyrenees. The southern group retreated to the southern edge of this belt, subsisting in



the Pyrenees Mountains and their foothills in southern France, in the southern Alps and in the Balkans. These conditions of isolation during last glaciations were considered to generate the two different varieties of *S. araneus* – the northern “*araneus*” type and the southern “*tetragonurus*” type (Dehnel, 1950).

However, our data do not support the idea that common shrews of “northern” and “southern” groups in the Ukraine represent different stocks with independent postglacial histories. It is known, that during the last glaciation maximum, a number of forest refugia with broad-leaved species remained in the central part of the Russian Plain (49–51° N), in the middle reaches of the Dniester and Don Rivers, in Moldova and near the Azov Sea (Simakova, 2001). Mishta (2005) assumed that colonization of northern and central parts of Eastern Europe could take place from different refugia located in the mid-continental part of the region rather than from the Mediterranean area or Crimea. The recent distribution of widespread chromosome races of the common shrew in Eastern Europe and analysis of environmental conditions during the last glacial period support the idea of the existence of such refugia (Markova *et al.*, 2001; Orlov & Kozlovskii, 2002). In the case of the Kiev and Neroosa races, it is likely that they were segregated before the last glacial maximum and maintained during glacial periods somewhere in refugia on either side of the Dnieper River (for example in the middle reaches of the Dniester and Don Rivers). After the glacial retreat, representatives of both races managed to occupy vast territories of Eastern Europe. It is noteworthy that the Dnieper River served as a natural barrier in the way of further expansion of both races.

The scenario of colonization of *S. araneus* in Eastern Europe and relationships between neighbouring races will be the subject of a future publication.

In the course of our investigation, we observed parallel geographic variation within two chromosome races of *S. araneus*, with increasing size in a southerly direction, along which there is a steep geoclimatic gradient. Moreover, this pattern has been found in other representatives of Soricidae (Mishta, 1997; Ochocińska & Taylor, 2003).

Modern analyses of geographic variation in a variety of species have demonstrated that subspecies designations are often dubious (Thorpe, 1975a, b, 1976, 1980, 1981a, b; Clover, 1979; Smith, 1979; López-Fuster & Ventura, 1987; Panteleev *et al.*, 1991; Panteleev, 1996). Many subspecies have been defined according to differences in exterior features only, without application of genetic criteria (because such techniques were not available at time of description). If such subspecies actually only differ in some features (such as body size) because of eco-geographical selection pressures, such taxa should be treated as ecotypes (Panteleev *et al.*, 2000).

As already demonstrated by comparison of condylobasal length in common shrews from many localities over its wide range, individuals are smaller in cold areas and, in general, larger in environments with high evapotranspiration (Ochocińska & Taylor, 2003).

Southern regions of Ukraine, in which the “southern” populations in this study were obtained, represent the Prichernomorie zoogeographical province of the Palearctic steppe subregion. The province is divided into two zones. The first zone includes river valleys, seacoasts and islands (hydrophyllous communities); the second one is field-steppe with artificial and natural islands of forests, forests belts and orchards (xerophilous communities) (Gizenko, 1965). So, in these regions the common shrew occurs specifically in river estuaries – reeds and marshes, surrounded by typical steppe vegetation. Due to this fact, and under the influence of specific climatic factors, “southern” shrews have acquired macro-morphological differences from “northern” shrews. Moreover, in this steppe southern limit of the species range, wet habitats to which the common shrew is confined are mainly isolated from each other. The morphological differentiation between neighbouring populations in the southern regions may be explained by this relative isolation of their habitats.

## Conclusion

No substantial differences in craniometric characters were revealed among the two main chromosome races of common shrews in the Ukraine. At the same time, within each chromosome race parallel clines of geographic variation can be seen. The extent of morphological differentiation of the common shrew populations is greater in the south. In other words, neighbouring groups of animals from northern, central, eastern and western Ukraine are less different than those in the south.

Intraspecific differentiation in the common shrew is significantly determined by high ecological plasticity and represents the response of the species to geoclimatic factors. Of top priority are temperature (average annual temperature of January and June, annual range of temperatures and annual number of days with temperature exceed 10°C) and precipitation (average snow depth, average annual precipitation). I consider it unhelpful to recognise separate subspecies in southern Ukraine and regard the different southern forms as ecotypes.

To avoid mixing concepts of geographical and racial differentiation, I recommend further investigations of macro-morphological variation and differentiation of *S. araneus* belonging to different chromosome races taking into consideration geoclimatic variation (especially by comparison of chromosome races which have an extensive range or with varied geographical origins). On the other hand, investigations on a smaller geographical scale may be more appropriate in studies of macro-morphological difference between chromosome races.

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Appendix 1. Mean values (upper row) and standard deviations (lower row) of 20 morphological variables (samples listed from north to south). Variables numbered as in Fig. 1.

Sample	Variables									
	1	2	3	4	5	6	7	8	9	10
Belarus (n=10)	19.37 0.286	2.61 0.047	5.39 0.121	3.99 0.083	9.75 0.216	8.06 0.213	5.59 0.142	1.38 0.059	2.57 0.088	4.63 0.139
Chernyiv (n=14)	19.47 0.353	2.55 0.083	5.39 0.129	3.92 0.091	9.75 0.114	8.27 0.141	5.80 0.064	1.37 0.049	2.83 0.102	4.63 0.072
Sumy (n=9)	19.19 0.304	2.60 0.088	5.31 0.121	3.84 0.076	9.55 0.218	8.20 0.141	5.72 0.087	1.37 0.079	2.71 0.145	4.65 0.104
Zhytomir (n=11)	19.19 0.304	2.57 0.068	5.37 0.168	3.96 0.120	9.49 0.199	8.15 0.180	5.68 0.134	1.38 0.071	2.56 0.092	4.60 0.125
Kiev (n=20)	18.98 0.314	2.57 0.095	5.47 0.139	3.89 0.122	9.66 0.205	8.00 0.159	5.77 0.228	1.34 0.062	2.61 0.109	4.68 0.124
Kaniv (n=20)	18.99 0.338	2.61 0.077	5.40 0.131	3.87 0.133	9.52 0.243	7.90 0.209	5.68 0.169	1.38 0.074	2.66 0.108	4.60 0.138

## Appendix 1 (continued).

Sample	Variables									
	1	2	3	4	5	6	7	8	9	10
Kharkiv (n=9)	19.06 0.350	2.56 0.099	5.38 0.151	3.93 0.105	9.67 0.164	8.19 0.215	5.53 0.193	1.41 0.086	2.63 0.101	4.56 0.063
Lugansk (n=20)	19.20 0.376	2.58 0.061	5.36 0.151	3.94 0.095	9.74 0.232	8.22 0.239	5.72 0.210	1.40 0.073	2.71 0.081	4.64 0.106
Karpaty (n=20)	19.48 0.237	2.61 0.059	5.32 0.122	3.88 0.078	9.69 0.233	8.21 0.173	5.75 0.146	1.38 0.068	2.77 0.101	4.66 0.069
Moldova (n=20)	19.52 0.293	2.59 0.110	5.56 0.140	3.93 0.096	9.65 0.287	8.45 0.169	5.94 0.166	1.43 0.057	2.70 0.086	4.86 0.100
Kherson (n=22)	20.43 0.321	2.65 0.147	5.56 0.157	4.09 0.141	9.96 0.176	8.67 0.213	6.15 0.183	1.47 0.063	2.90 0.068	4.90 0.088
Golaya Pristan' (n=12)	19.92 0.33	2.60 0.09	5.57 0.07	4.12 0.09	9.98 0.11	8.42 0.17	6.03 0.30	1.45 0.05	2.73 0.12	4.91 0.10
Odessa (n=25)	20.44 0.319	2.77 0.111	5.73 0.164	4.10 0.126	10.01 0.200	8.88 0.332	5.97 0.177	1.43 0.079	2.75 0.100	5.00 0.121
Romania (n=20)	20.69 0.318	2.75 0.091	5.75 0.138	4.14 0.110	10.12 0.171	8.89 0.230	5.92 0.129	1.44 0.054	2.78 0.119	4.89 0.118
	11	12	13	14	15	16	17	18	19	20
Belarus (n=10)	3.91 0.139	5.50 0.123	3.83 0.074	1.72 0.040	7.41 0.234	0.56 0.056	1.02 0.175	6.93 0.217	4.82 0.153	1.08 0.068
Chernyiv (n=14)	3.93 0.074	5.51 0.080	3.88 0.062	1.78 0.056	7.42 0.123	0.59 0.037	1.02 0.123	6.93 0.216	4.77 0.100	1.05 0.045
Sumy (n=9)	3.83 0.178	5.56 0.101	3.88 0.076	1.73 0.048	7.42 0.188	0.58 0.069	1.09 0.095	6.98 0.145	4.73 0.048	1.12 0.061
Zhytomir (n=11)	3.89 0.117	5.45 0.084	3.83 0.075	1.71 0.054	7.26 0.123	0.54 0.058	1.10 0.067	6.79 0.152	4.66 0.114	1.08 0.056
Kiev (n=20)	3.86 0.179	5.45 0.146	3.89 0.108	1.75 0.094	7.34 0.182	0.55 0.079	1.07 0.085	6.82 0.166	4.75 0.124	1.08 0.086
Kaniv (n=20)	3.82 0.116	5.44 0.122	3.82 0.112	1.73 0.071	7.30 0.192	0.52 0.048	1.03 0.099	6.81 0.172	4.68 0.139	1.05 0.081
Kharkiv (n=9)	3.76 0.135	5.42 0.083	3.75 0.097	1.68 0.078	7.25 0.228	0.60 0.055	1.07 0.103	6.93 0.157	4.65 0.187	1.10 0.095
Lugansk (n=20)	3.91 0.087	5.54 0.098	3.84 0.089	1.71 0.038	7.38 0.137	0.56 0.055	1.07 0.137	6.99 0.137	4.68 0.139	1.09 0.056
Karpaty (n=20)	4.00 0.117	5.59 0.091	3.91 0.087	1.78 0.056	7.41 0.183	0.51 0.053	1.00 0.147	6.95 0.152	4.79 0.089	1.11 0.083
Moldova (n=20)	3.95 0.145	5.72 0.073	4.03 0.068	1.83 0.041	7.59 0.140	0.53 0.054	1.12 0.119	7.06 0.114	4.86 0.094	1.15 0.069
Kherson (n=22)	4.15 0.115	5.82 0.069	4.07 0.063	1.84 0.048	7.86 0.139	0.70 0.065	1.10 0.097	7.43 0.154	5.12 0.151	1.24 0.062
Golaya Pristan' (n=12)	3.96 0.10	5.71 0.07	4.01 0.05	1.78 0.05	7.56 0.15	0.61 0.04	1.07 0.08	7.28 0.14	4.94 0.150	1.22 0.08
Odessa (n=25)	4.08 0.141	5.87 0.136	4.11 0.087	1.88 0.059	7.83 0.188	0.65 0.058	1.07 0.152	7.35 0.169	4.98 0.129	1.14 0.065
Romania (n=20)	4.04 0.112	5.87 0.096	4.05 0.093	1.82 0.042	7.87 0.188	0.60 0.058	1.08 0.151	7.48 0.196	5.05 0.102	1.16 0.064

Appendix 2. Loadings for principal components based on craniometric variables.

Variable	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
1	-0.916	-0.044	0.067	-0.059	0.123	-0.089
2	-0.635	0.335	0.454	-0.033	0.195	0.174
3	-0.776	-0.236	-0.176	-0.149	-0.119	0.174
4	-0.589	0.141	0.415	-0.225	0.243	-0.110
5	-0.731	0.161	0.293	-0.132	-0.009	0.111
6	-0.875	-0.030	-0.018	-0.078	0.083	-0.216
7	-0.664	-0.044	-0.119	0.010	-0.257	0.410
8	-0.444	-0.455	0.030	0.006	0.479	0.185
9	-0.555	-0.432	0.240	0.291	0.206	-0.097
10	-0.860	-0.010	-0.004	-0.193	-0.165	-0.029
11	-0.635	-0.515	0.059	0.028	-0.003	0.169
12	-0.912	-0.096	-0.058	-0.144	-0.067	-0.080
13	-0.841	-0.106	-0.082	-0.264	-0.254	-0.067
14	-0.699	-0.192	-0.179	-0.192	-0.375	-0.003
15	-0.893	0.071	-0.197	0.001	0.063	-0.134
16	-0.504	0.213	0.057	0.487	-0.215	-0.412
17	-0.147	0.570	-0.619	-0.275	0.315	0.049
18	-0.854	0.119	-0.117	0.056	0.163	-0.238
19	-0.812	0.068	-0.104	0.101	0.086	0.169
20	-0.491	0.243	-0.203	0.558	-0.064	0.291

Appendix 3. Loadings for canonical functions based on (a) craniometric and (b) geoclimatic variables.

a)

Variable	MORPH 1	MORPH 2	MORPH 3	MORPH 4	MORPH 5
1	-0.376	0.140	-0.135	0.608	-1.775
2	-0.005	-0.451	-0.329	0.061	-0.197
3	-0.139	0.499	-0.466	0.491	0.565
4	-0.037	0.204	0.160	-0.002	-0.331
5	0.091	-0.205	0.637	0.126	0.488
6	-0.217	-0.407	-0.062	-1.336	0.258
7	-0.110	0.126	-0.045	0.113	0.200
8	-0.087	-0.215	-0.148	-0.131	0.408
9	0.120	-0.017	0.475	0.160	0.145
10	-0.112	0.074	-0.338	-0.034	0.376
11	0.039	0.018	0.315	0.193	0.115
12	-0.085	-0.091	0.805	-0.839	-0.035
13	0.033	0.259	-0.649	0.104	-0.026
14	-0.102	0.295	0.057	0.017	-0.224
15	0.224	0.387	-0.088	-0.142	-0.315
16	-0.036	-0.558	-0.395	0.305	-0.284
17	0.027	-0.229	-0.051	-0.253	-0.017
18	-0.273	-0.413	0.252	0.602	0.826
19	-0.007	0.276	-0.045	0.254	-0.083
20	-0.127	-0.146	0.191	-0.226	0.308

b)

Variable	GEOCL 1	GEOCL 2	GEOCL 3	GEOCL 4	GEOCL 5
LONG	0.185	-0.654	-0.530	1.297	1.617
LAT	0.096	-2.071	-1.140	0.701	-0.821
ALT	-0.190	-2.413	-0.604	-0.819	-0.824
TEMP_J	-1.569	-1.274	-3.375	2.987	0.999
TEMP_I	-1.923	-2.305	-0.127	0.075	-1.330
TEMP_D	2.586	2.120	2.963	-0.829	1.239
W_DAYS	-0.329	-0.447	0.356	0.781	-1.216
SNOW	0.332	1.581	1.282	2.196	0.886
RAIN	-0.431	-0.015	0.477	0.674	0.039